Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment

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Abstract: The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most vibrant research fields in ecology and environmental sciences over the past two decades. Hundreds of experiments have now manipulated species diversity to test its effects on a wide range of ecosystem properties. Methods that partition the effect of functional complementarity between species from that of selection for species with particular traits have been instrumental in clarifying the results of these experiments and in resolving debates about potential underlying mechanisms (Loreau and Hector 2001, Cardinale et al. 2007). Relatively few studies, however, have sought to disentangle the actual biological mechanisms at work in the effects of biodiversity on ecosystem functioning. Yet theory shows that different coexistence mechanisms can lead to different BEF relationships (Mouquet et al. 2002). Understanding the mechanisms that drive the functional consequences of biodiversity and their connections with those that determine the maintenance of biodiversity is key to making BEF research more predictive and more relevant to natural, non-experimentally manipulated ecosystems (Loreau 2010). The recent theoretical study by Carroll, Cardinale, and Nisbet (2011; hereafter CCN) makes a valuable contribution toward the goal of linking the maintenance of diversity and its functional consequences. CCN use MacArthur's (1972) classical consumer

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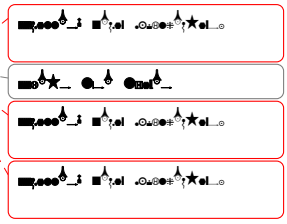

The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most vibrant research fields in ecology and environmental sciences over the past two decades. Hundreds of experiments have now manipulated species diversity to test its effects on a wide range of ecosystem properties. Methods that partition the effect of functional complementarity between species from that of selection for species with particular traits have been instrumental in clarifying the results of these experiments and in resolving debates about potential underlying mechanisms (Loreau and Hector 2001, Cardinale et al. 2007). Relatively few studies, however, have sought to disentangle the actual biological mechanisms at work in the effects of biodiversity on ecosystem functioning. Yet theory shows that different coexistence mechanisms can lead to different BEF relationships (Mouquet et al. 2002). Understanding the mechanisms that drive the functional consequences of biodiversity and their connections with those that determine the maintenance of biodiversity is key to making BEF research more predictive and more relevant to natural, non-experimentally manipulated ecosystems (Loreau 2010).

intimate

The recent theoretical study by Carroll, Cardinale and Nisbet (2011) (hereafter CCN) makes a valuable contribution toward the goal of linking the maintenance of diversity and its functional consequences. CCN use MacArthur's (1972) classical consumer–resource model to develop new measures of niche difference (ND) and relative fitness difference (RFD) between consumers. They then explore the relationships between these new measures and the widely used additive partition (AP) of the net biodiversity effect into a complementarity effect (CE) and a selection effect (SE), as well as the relative yield total (RYT), a measure closely related to CE (Loreau and Hector 2001). Their analysis leads them to conclude that "post hoc statistical methods currently used to discern the mechanisms that drive effects of diversity on biomass do not necessarily reflect real biological processes that relate to mechanisms of species coexistence". This conclusion serves as a

existing literature

in this context

reminder that, however useful, no post hoc analysis will ever be able to replace detailed knowledge of the biological mechanisms at work.

But CCN also suggest that the ND and RFD metrics they devise are more appropriate than AP for identifying mechanisms that drive BEF relationships; accordingly, they propose that future theoretical and empirical work should focus on "predicting community biomass from three independent variables: ND, RFD, and species richness". As we explain below, we feel that these additional conclusions are unwarranted; they are based on the implicit assumption that CCN's new approach is intrinsically better than AP without any independent demonstration that it does in fact do a better job. On the other hand, CCN's study raises valid questions about the scope and limitations of AP, which has been sometimes liberally interpreted in the recent literature. In this comment, therefore, we would like to (1) revisit the scope and limitations of the AP approach, (2) discuss some of the limitations of CCN's new proposed approach, and (3) briefly suggest some directions that could be taken to move BEF research forward.

When two of us proposed AP ten years ago (Loreau and Hector 2001), it was in the context of a raging debate about the interpretation of BEF experiments (Loreau et al. 2001). The main interest of this approach was to allow testing of hypotheses that assume changes in numerical dominance among species but no functional complementarity, such as the much-debated "sampling effect" and "mass ratio" hypotheses. Essentially, these hypotheses propose that changes in community production or biomass can be explained simply by zero-sum changes in the relative abundances of species in mixture. The alternative — that communities are more (or less) than the sum of their parts — has for a long time been termed overyielding (or underyielding). AP has played a valuable role for testing these types of null hypothesis via its two components, SE and CE.

SE is a straightforward application of a basic statistical approach: it is a covariance term that relates the performance of a species in mixture (whether its relative yield increases or decreases relative to expectations) to its monoculture biomass. It is positive when species with large monoculture biomasses on average perform better in mixtures, and negative when the reverse is true. When changes in relative abundances follow a zero-sum game, then SE (whatever its sign) will explain the effects of diversity on mixture yield. Ecologists are familiar with covariances and correlations; thus SE is relatively simple and easy to understand.

CE quantifies overyielding, i.e., an increase in mixture yield above the zero-sum expectation (or underyielding when mixtures produce less than expected), which provides a simple, operational way to define functional complementarity by its net effect at the community level. Although technically CE has the dimension of absolute yield, one advantage is that it is closely related to the relative yield and RYT concepts used in plant ecology and intercropping since the 1950s and they are therefore once again familiar to ecologists and relatively well understood. In addition, CE and RYT have the nice property of being directly connected to the conditions for stable coexistence in the classical Lotka-Volterra competition model (Vandermeer 1981, Loreau 2004).

In total, the AP and RYT frameworks are relatively simple and based on long-established methodologies that are familiar to many ecologists. We therefore feel that, despite their limitations, they will continue to have great value for performing tests of null hypotheses such as the sampling effect and mass ratio hypotheses, and for generating alternative hypotheses about possible mechanisms underlying BEF relationships detected in experiments.

It is important to note, however, that CE and RYT do not provide quantitative measures of resource partitioning because they potentially combine the effects of a wide range of species interactions, as one of us established clearly (Loreau 1998). A positive CE (or, equivalently, RYT

92 > 1) means that niche differentiation (partitioning of either resources or natural enemies), positive
93 interactions, or some combination thereof, are strong enough to outweigh interference competition
94 or other negative species interactions that might decrease relative yields in mixture. Conversely, a
95 negative CE (or RYT < 1) indicates that negative species interactions are strong enough to
96 outweigh the positive effects of niche differentiation and positive interactions on relative yields in
97 mixture. Thus, AP was devised as a tool to test hypotheses, not as a tool to identify the type and
98 strength of species interactions. It is the sign and relative magnitude of CE and SE that matter in
99 hypothesis testing, while their absolute magnitudes should be interpreted more cautiously because
100 of the range of biological processes that can affect them.

101 Liberal interpretations of AP as a means to identify and quantify species interactions may
102 have resulted from ambiguous usage of the term "mechanism" in the BEF literature as well as in
103 other areas of ecology. A "mechanism" denotes any lower-level process that contributes to
104 generating a higher-level "phenomenon" of interest. In this sense, although CE and SE, the two
105 components of AP, provide information about which mechanisms are compatible with the
106 observed effects of biodiversity on ecosystem functioning, they do not themselves correspond to
107 particular biological mechanisms because they combine the effects of a potentially wide range of
108 individual-level processes on the community-level phenomenon of yield, hence their appropriate
109 designation as "effects". The literature, however (including Loreau and Hector 2001), has often
110 used the terms "mechanisms", "classes of mechanisms" or "types of mechanisms" to describe CE
111 and SE, leading sometimes to the improper interpretation that they quantify individual-level
112 biological processes. Just as with any other approach, greater terminological and conceptual clarity
113 is likely to help better appreciate the scope and limitations of AP.

114 The new approach proposed by CCN relies on an attempt to formalize Chesson's (2000)
115 conceptual distinction between stabilizing and equalizing coexistence "mechanisms". They build

measures of ND and RFD that capture these two "mechanisms" based on the sensitivities of species' invasion rates to interspecific competition. Specifically, ND is measured as one minus the geometric mean of these sensitivities, while RFD is measured as their geometric standard deviation. CCN then show that both increasing ND and decreasing RFD increases RYT and CE, in contrast to their intuitive expectations that only ND should affect RYT and CE based on the assumption that the latter measure resource partitioning between species. This particular result leads them to conclude that current measures of functional complementarity "give a largely skewed estimate of resource partitioning". There are, however, several fundamental problems with this interpretation.

The first problem follows directly from the above discussion of the concept of "mechanism". While Chesson's distinction is useful to identify two types of constraints that affect coexistence, we know of no evidence that these constraints reflect independent biological processes, and hence that they correspond to distinct biological mechanisms. Just as with CE and SE, the so-called stabilizing and equalizing "mechanisms" define effects at the community level (specifically, on coexistence); these effects also summarize a wide range of species interactions, including resource partitioning, natural enemy partitioning, facilitation, and interference. Even in the specific context of consumer–resource interactions considered by CCN, deterministic niche differences between species include differences in niche height (absolute level of resource consumption), niche breadth, and niche overlap. Differences in niche height and niche breadth are usually implicitly related to RFD, while low niche overlap is usually associated with ND (despite the fact that niche overlap is only one component of niche differences) because it is a necessary condition for stable coexistence. Differences in niche height and niche breadth, however, also affect quantitative measures of niche overlap and the amount of niche overlap that is necessary to allow coexistence. Therefore, except in special cases, ND and RFD should be expected to reflect the operation of a

number of overlapping lower-level processes. Thus, our first conclusion is that AP and the distinction between stabilizing and equalizing "mechanisms" — or, more appropriately, effects — are two alternative ways to sort the community-level effects of individual-level mechanisms.

A second conclusion follows immediately from the first. Since the two alternative frameworks provide different ways to define and aggregate the community-level consequences of individual-level processes and since they work with different quantities (sensitivity of invasion rates to interspecific competition vs. yield), it is hardly surprising that they produce different results. The fact that both ND and RFD affect CE and SE can be no more an argument for rejecting the latter than the reciprocal fact that both CE and SE affect ND and RFD would be an argument for rejecting ND and RFD. Therefore, without some independent confirmation, CCN's results neither justify their suggestion that ND and RFD are more appropriate than AP for identifying mechanisms that drive the BEF relationships, nor do they support their claim that CE gives a skewed estimate of resource partitioning.

This brings us to a third issue — the specific limitations of the ND and RFD metrics within the context of BEF research. In contrast to AP, which was tailored to test hypotheses about the effects of biodiversity on yield, ND and RFD bear no necessary relation to yield and other ecosystem properties that are measured in biodiversity experiments. The simple relationships that are often assumed between community-level resource depletion, production, and biomass at equilibrium hold only under restricted conditions that may apply to annual plants but not necessarily to other organisms (Loreau 2010). The connections between these equilibrium properties and the sensitivity of species' invasion rates to interspecific competition are bound to be even weaker because the traits that govern a species' ability to invade a subset of a community are not necessarily the same as those that govern its yield once established in the full community. There is mounting evidence that the strength of trophic interactions depends on the presence and

density of other species and that these trophic interaction modifications themselves interact (Golubski and Abrams 2011), generating a plethora of higher-order density-dependent effects in communities. For instance, Bogran et al. (2002) demonstrated phenotypic plasticity in host use by parasitoids along two niche axes, such that parasitoid species that appear redundant when studied independently may become complementary when they coexist. In such cases, niche differences measured using invasion rates have little to do with overyielding detected in biodiversity experiments. Experimental evidence also suggests that both the magnitude and the nature of biodiversity effects may change over time (Cardinale et al. 2007). Thus, while sensitivities of invasion rates are useful within the context of coexistence theory, it is doubtful that they will generally provide robust predictors of equilibrium ecosystem properties. It is also unclear how ND and RFD can be used to test some of the basic hypotheses of interest in BEF research. For instance, the sampling effect hypothesis assumes specifically that the species with the highest monoculture yield or carrying capacity outcompetes the others in mixtures. ND and RFD are unable to test this hypothesis because they are independent of the absolute value of carrying capacities (Appendix). For all these reasons, it seems to us that the AP approach has a distinct practical advantage for hypothesis testing in biodiversity experiments.

Lastly, the results reported by CCN are largely restricted to 2-species systems, with some additional simulations for 3 and 4 species. Although the general trends they reveal seem to be robust, they should not mask some significant deviations from these trends, which confirm that ND and RFD bear no simple relations to overyielding, and hence that their use as tools to interpret biodiversity experiments would require more careful examination. In particular, CCN's central result that RYT (and hence CE) increases as ND increases and as RFD decreases does not always hold, even within the restricted scope of MacArthur's model. For some scenarios and parameter values, opposite patterns can be found.

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To illustrate and understand this possibility, we use the continuous formulation of MacArthur's model because it provides an explicit measure of niche differences (*sensu* niche overlap) between species along a resource gradient (Sapijanskas and Loreau 2010), and we focus on the specific example of 4 consumer species distributed in 2 functional groups. For simplicity, we assume that the two species in each functional group i have the same niche width, σ_i, and that the two functional groups are different enough (i.e., are spread out enough along the resource gradient) that competitive interactions between groups is negligible. In this case, ND, RFD and RYT can be obtained analytically (Appendix):

easily

$$ND = 1 - \exp\left[-\frac{1}{8}\left(\frac{\Delta_1^2}{\sigma_1^2} + \frac{\Delta_2^2}{\sigma_2^2}\right)\right], \tag{1}$$

$$RFD = \exp\left\{\frac{1}{8}\sqrt{\left(\frac{\Delta_1^2}{\sigma_1^2} - \frac{\Delta_2^2}{\sigma_2^2}\right)^2 + 32\left[\left(\log\frac{K_{1a}}{K_{1b}}\right)^2 + \left(\log\frac{K_{2a}}{K_{2b}}\right)^2\right]}\right\}, \tag{2}$$

$$RYT = \frac{2 - \exp\left(-\frac{\Delta_1^2}{4\sigma_1^2}\right)\left(\frac{K_{1a}}{K_{1b}} + \frac{K_{1b}}{K_{1a}}\right)}{1 - \exp\left(-\frac{\Delta_1^2}{2\sigma_1^2}\right)} + \frac{2 - \exp\left(-\frac{\Delta_2^2}{4\sigma_2^2}\right)\left(\frac{K_{2a}}{K_{2b}} + \frac{K_{2b}}{K_{2a}}\right)}{1 - \exp\left(-\frac{\Delta_2^2}{2\sigma_2^2}\right)}, \tag{3}$$

where K_{ia} and K_{ib} are the carrying capacities of the two species in functional group i, and Δ_i is the distance between their niche centres along the resource gradient.

As expected, ND decreases exponentially as niche overlap within functional groups increases (remember that niche overlap between functional groups is assumed to be negligible). RFD has two components: the first term under the square root in equation (2) is a measure of the difference between the two functional groups in the amount of niche overlap within the group, while the second is a measure of competitive dominance within the groups. Note that niche overlap affects both ND and RFD, such that the two measures are not independent from each

other, as we suggested above based on intuitive arguments. But niche overlap and competitive dominance interact more strongly in RYT since the relative yield total of each functional group weighs the effect of niche overlap by competitive imbalance such that decreased niche overlap has a disproportionately larger positive effect when species are competitively dissimilar (i.e., when $K_{ia}/K_{ib} + K_{ia}/K_{ib}$ is larger). Since RYT incorporates the effects of niche overlap and competitive imbalance in different ways than do ND and RFD, all sorts of relationships between these measures are possible, including relationships that are opposite to those found by CCN — i.e., RYT can decrease, rather than increase, as ND increases and as RFD decreases (Fig. 1). Note that these findings do not prove that there is anything intrinsically wrong with the approach based on ND and RFD. But they do challenge the use of these metrics as some sort of self-evident reference against which RYT and AP should be assessed. We see no justification for assuming the superiority of the first approach over the second.

Where does all this leave the BEF research field? Methods based on relative yield, in particular AP, have been the primary tool used in identifying biodiversity effects over the last 10–15 years. CCN's study reiterates that CE cannot be directly equated to resource partitioning, and shows that CE and SE do not correspond to stabilizing and equalizing coexistence effects. This is not surprising because CE and SE were not developed to quantify resource partitioning or coexistence mechanisms. Instead, CE and SE are useful tools to test hypotheses. For example, Cardinale (2011) used AP in the analysis of a recent experiment where SE and CE appear to do a good job in identifying the signatures of species dominance and complementarity, respectively. Unfortunately, the ND and RFD measures proposed by CCN are also unable to quantify biological processes such as resource partitioning because, like CE and SE, they are net measures of multiple biological processes. Thus, it is unclear how they can contribute to enhance our ability to detect biological mechanisms.

231 Given the limitations inherent in all pre-existing post hoc statistical methods (reviewed in
232 Hector et al. 2009) and CCN's new approach, how can we make further progress in understanding
233 the mechanisms that explain the maintenance of biodiversity and its functional consequences? We
234 believe that such progress requires at least two key ingredients. The first is expanding theory that
235 connects the microscopic mechanics of species interactions and the macroscopic properties of
236 whole ecosystems. There have been recent developments in this area (Loreau 2010), and we
237 welcome CCN's work as a new contribution toward this shared goal. The main challenge for
238 theory development will be to keep a unifying perspective while examining the mechanistic details
239 of species interactions. The distinction between stabilizing and equalizing coexistence effects
240 provides one possible unifying framework, but others are conceivable. One of the important roles
241 of ecological theory should be to build and explore alternative unifying frameworks that link the
242 microscopic and macroscopic properties of ecosystems. Second, we need a new generation of
243 experiments that analyze the individual- and population-level processes that generate the effects of
244 biodiversity on ecosystem functioning. When two of us proposed the AP methodology (Loreau
245 and Hector 2001), we concluded that this methodology "cannot replace direct experimental
246 investigations into the mechanisms at work in responses to biodiversity changes at the ecosystem
247 level, which are now critical to further progress in this area". This conclusion is still topical today.
248 A few pioneering studies have experimentally manipulated available niche space
249 (Dimitrakopoulos and Schmid 2004, Cardinale 2011) or species' niches through evolution (Gravel
250 et al. 2011) to test for the role of resource partitioning in shaping BEF relationships. Others have
251 manipulated intra- and interspecific population densities simultaneously to disentangle the roles of
252 resource partitioning and facilitation in overyielding (Gross et al. 2007, Northfield et al. 2010).
253 Still others have manipulated the presence of mutualists (van der Heijden et al. 1998) or pathogens
254 (Maron et al. 2011, Schnitzer et al. 2011) to test for their role in driving BEF relationships. But

overall the number of studies that have tested underlying mechanisms explicitly is still too limited to draw general conclusions on the lower-level processes that drive BEF relationships and the way these processes interact. Combining innovative theory and experiments that allow us to disentangle these processes and bring them together in a coherent unifying framework should now be a major research focus in community and ecosystem ecology.

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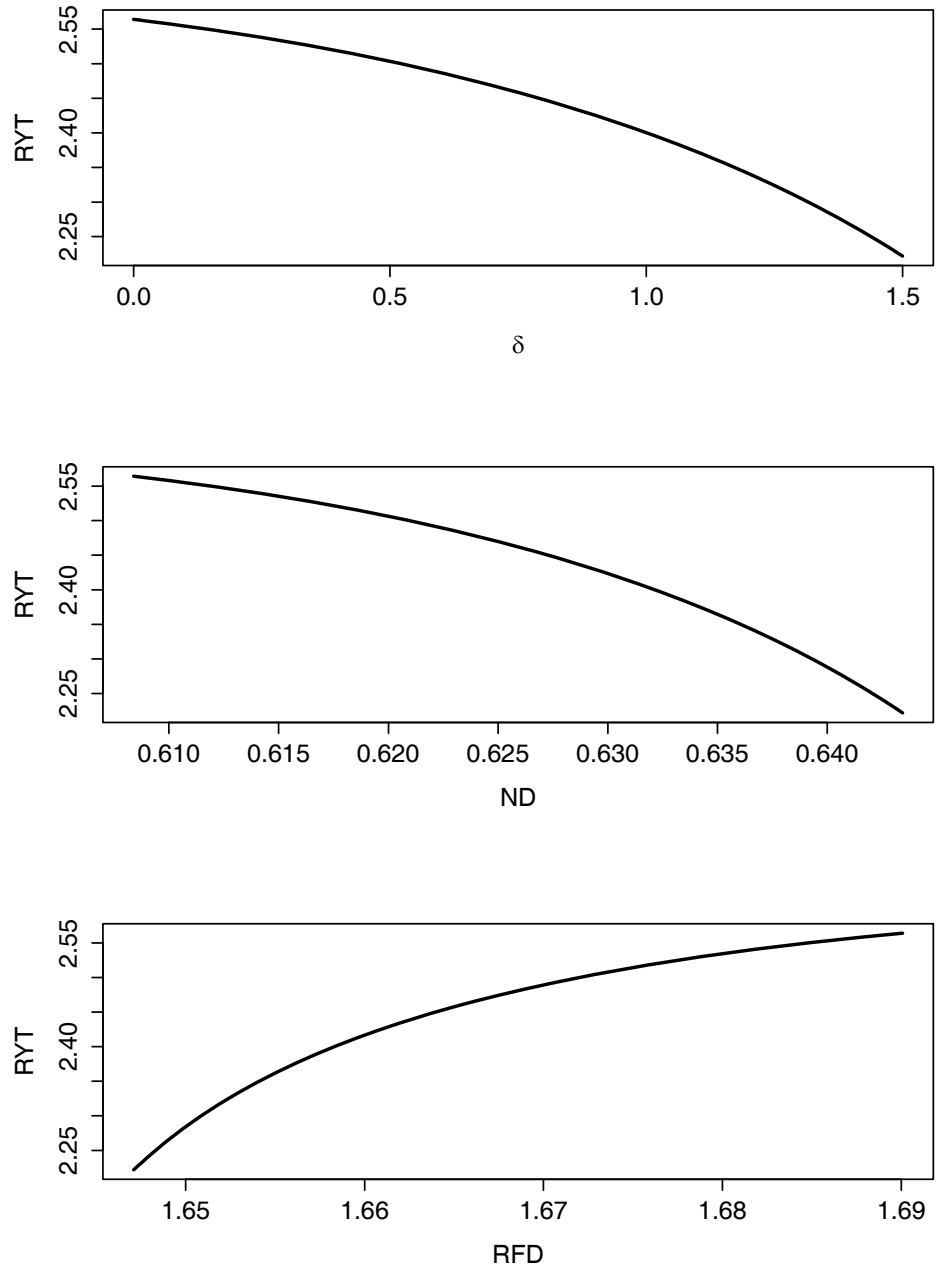
Figure legend

Fig. 1. Changes in the relative yield total, RYT, and the resulting relationships between RYT and ND or RFD when niche overlap varies in a community of 4 species distributed in 2 functional groups (equations 1–3). Niche overlap is here varied in opposite directions in the two functional groups using the transformation $\left\{\frac{\Delta_1^2}{\sigma_1^2}, \frac{\Delta_2^2}{\sigma_2^2}\right\} \rightarrow \left\{\frac{\Delta_1^2}{\sigma_1^2} - \delta, \frac{\Delta_2^2}{\sigma_2^2} + 1.5\delta\right\}$, where δ is increased from an initial value of zero. Parameters were chosen such there is both greater niche overlap ($\Delta_1/\sigma_1 < \Delta_2/\sigma_2$) and greater competitive imbalance ($K_{1a}/K_{1b} + K_{1b}/K_{1a} > K_{2a}/K_{2b} + K_{2b}/K_{2a}$) in the first functional group. ND and RFD are increasing and decreasing functions, respectively, of δ. Yet, RYT decreases with δ because the competitive imbalance between the two groups is sufficiently large for the positive effect of reduced niche overlap in the second group ($\Delta_2^2/\sigma_2^2 + 1.5\delta$) to overwhelm the negative effect of increased overlap in the first ($\Delta_1^2/\sigma_1^2 - \delta$) (Appendix). In this example, $\Delta_1^2/\sigma_1^2 = 3$, $\Delta_2^2/\sigma_2^2 = 4.5$, $K_{2a} = K_{2b}$, and $K_{1a} = 2K_{1b}$. Stable coexistence of the four species requires $\delta < 1.4$.



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339 **Figure 1**